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4531

UNITED STATES DEPARTMENT OF AGRICULTURE
AGRICULTURAL RESEARCH ADMINISTRATION
BUREAU OF ENTOMOLOGY AND PLANT QUARANTINE

Project | Date April 14, 1952 | Author

SUBJECT—

TITLE

THE ROLE OF QUANTITATIVE OLEORESIN PRODUCTION IN THE SUSCEPTIBILITY OF PINES TO BARKBEETLES

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U. S. GOVERNMENT PRINTING OFFICE 16—47272-1

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THE ROLE OF QUANTITATIVE OLEORESIN PRODUCTION IN THE SUSCEPTIBILITY OF PINES TO BARKBEETLES

A new theory in explanation of the apparent host selection by the western pine beetle has recently been presented (Callaham, 1952). This theory has been formulated primarily as a result of investigations conducted at the Institute of Forest Genetics, Placerville, California by John M. Miller, Entomologist, and the author. The essence of this theory is that the adult beetles make their first attacks at random throughout the forest and that the success or failure of these attacks on any particular tree is determined by the quantitative oleoresin production of the trees; thus, if the resin flow is of sufficient quantity and continues for a length of time necessary to exhaust the energy potential of the beetle, then the attack will be "pitched out". On the other hand, if the resin flow stops, allowing the beetle pair to start an egg gallery through the phloem, then the attack will be successful and fermentative reactions will be initiated which will attract other beetles to the tree.

Essentially this is the oleoresin theory of bark-beetle susceptibility, and the subject of this paper is to discuss (1) the theoretical principles of oleoresin production in pines, (2) the various factors which determine quantitative production, and (3) the possible use of this information in studying the susceptibility of pines to bark beetles. With this in mind, it seems logical to discuss, first, the general principles which govern oleoresin production in all pine species.

Principles Governing the Production of Oleoresin in all Pine Species

An extensive review has been made of the great mass of literature pertaining to oleoresin production in most of the genera of the Pinaceae. This literature can be separated into two major categories - (1) the anatomical approach and (2) the physiological approach to the problem. The greatest amount of effort has been directed toward ontogenetic and morphological studies of the resin systems of needles, twigs, stems, and roots, and although comparatively little has been done on the physiological approach to the problem, it is this latter approach which has contributed the most to our present understanding of the basis of oleoresin production. In the two following sections of this report the present knowledge of each of these two phases will be briefly summarized.

The Anatomical Basis of Oleoresin Production

An extensive body of literature pertaining to this subject has accumulated during the years since the latter part of the 17th century

when Malpighi and Grew first noticed resin ducts as a part of the morphology of numerous plants. Tschirch (1906) in his voluminous treatise presents an excellent review of the literature published prior to the 20th century, but at the present time there is a great need for a bibliography of the current literature on oleoresin systems and oleoresin production.

In general the internal anatomy of the xylem of the pine species used for turpentining is very similar from one species to another (Brown, et al. 1949). The structure of resin ducts is the same in all pine species. The longitudinal ducts usually are 100-200 microns in diameter and 1/2 to 1 meter in length (Munch, 1921). The transverse ducts, which are found in the center of 3- to 4-seriate rays, are from 50 to 100 microns in diameter and attain a maximum length equal to the radius of the stem. Both longitudinal and transverse ducts have essentially the same ontogeny and morphology.

There is a single layer of epithelial cells surrounding the central resin canal into which resin is secreted. These epithelial or excreting cells only have primary walls, and they are reported to have no pits (Munch) although primary pit fields may be present. These cells also have abundant protoplasm, reserve material, and a large nucleus. Their peripheral walls are stronger than normal parenchyma cell walls. When these cells are turgid, they are vesicular and fill the resin canal, but when the canal is filled with resin, they are compressed. In this latter case the radial walls are oblique and folded.

Surrounding the secreting cells is a cylinder of dead, flattened, parenchymatous cells. These are free of any material except occasional water and are usually filled with air. These are referred to as the sheath cells (Munch). They always are radially compressed with the radial walls folded or pulled apart. This results from the compression of the sheath cells by the secreting cells during the schizogenous development of the duct. Ivanov (1930) reports that the walls of these cells are lignified. The sheath cells do not always form a continuous circle around the secreting cells. In the case of the transverse ducts they often are found only on the radial walls of the ducts. However, the sheath cells are important physiologically because, as dead elements, they reduce the exchange of material between the secreting cells and their environment of tracheary elements.

The concentric cylinders of secreting and sheath cells are further surrounded by a cylinder of ordinary, longitudinal, parenchyma cells, which Munch called companion cells of the resin duct. These cells, if not dead and compressed like sheath cells, are rich in protoplasm and reserve materials. The latter are in the form of oil drops and starch granules. Although no pits are to be found in the resin duct itself, the companion cells frequently are connected with the surrounding tracheary elements, tracheids and septate-tracheids, by means of half-bordered pit pairs.

According to Mayr (1884) the transverse ducts originate from the longitudinal ducts; however, Kirsch (1911) is of the opinion that the

reverse is true. Regardless of which is the proper interpretation, it generally is recognized that these two systems are interconnected at their intersection and that by this means the resin stored in the longitudinal canals can be carried through the cambium and phloem to the tangential surface of any wound.

The Physiological Basis of Resin Production

Most of the original work on the determination of the physiological principles underlying quantitative oleoresin production was carried out in Europe in connection with turpentining experiments in Germany (Munch) and Russia (Ivanov). Similar work has been done more recently in the southern pine regions of this country. Because of the anatomical uniformity of most pine species and the similarity of results obtained from turpentining experiments in different regions of the world, it seems logical that the results of these studies can be applied to the pine species of the western United States. However, one must realize that no specific work of this type has been attempted on our western species.

The studies of Munch and Ivanov have shown that there are two general conditions affecting quantitative oleoresin production of each resin duct. These are (1) the factors which affect the rate of flow of resin from the severed canal and (2) the factors which affect the rate of resin formation in the resin duct.

Factors affecting the rate of resin flow - the factors which affect the rate of flow from the severed canal are the following: (a) viscosity of the resin and (b) osmotic pressure of the epithelial cells forcing the gum out of the canals. The former is a function of the temperature of the moisture columns of the tree and of the air at the cut surface of the canal. The latter is a function of the degree of compression of the epithelial cells and the availability of water to the epithelial cells. It should be stressed at this point that resin will not flow from a severed resin canal unless it is forced out by the expansion of the epithelial cells. Friction also probably plays some role in resin flow, but as yet this is not clearly understood.

As one considers these factors, it is obvious that the highest rate of resin flow would be obtained when the temperature of the water columns and outside air was high, when the resin canals were filled to the maximum, and when the physical tension of the water column was reduced under conditions of adequate soil moisture, dilute sap solution, and high relative humidity. Conversely, the resin flow would diminish with decreasing temperature, and it would finally cease if the average 24-hour temperature fell below 12°C (Munch). The resin flow also would diminish if the canals were not completely filled and if the moisture tensions within the stem were high enough to exceed the osmotic pressure of the epithelial cells making it impossible for these cells to absorb water through their air jacket. Thus, in the latter condition the cells could not become distended and could not force the resin out of the canals.

Factors affecting the rate of resin formation - regardless of the rate of flow of resin, the factors which affect the rate of resin formation in the resin duct are (a) the osmotic pressure of the epithelial cells (b) the temperature of water available to these cells, (c) the actual availability of water to these cells and (d) the availability of nutrients to these cells. Thus, the maximum resin production is attained when the epithelial cells are completely distended, when their osmotic pressure is reduced, and when there is an adequate movement of comparatively warm water through the air-filled jacket cells into the epithelial cells, and when their cell contents contain a sufficient supply of the nutrients necessary for resin synthesis. The probability that this latter point has some influence on resin formation has been emphasized time and again, but as yet no conclusive studies have been carried out to investigate the biochemistry of resin synthesis.

Predetermining the Rate of Resin Flow

From the imposing list of variables given in the preceding section, it is quite obvious why it has been impossible to predetermine on a theoretical basis the rate of resin flow from a given tree or to account for the tree to tree variations in quantitative yield. However, investigators working on slash pine at the southeastern Forest Experiment Station (Schopmeyer and Mergen, 1952) have found in actual practice that there is a very high correlation between the rate of resin flow during the first twenty-four hours after wounding and a modification of Poiseuille's law, including the following three independent variables: (1) viscosity of gum, (2) number of radial resin ducts per unit area of tangential surface, and (3) the square of the mean cross-sectional area of the radial resin ducts.

Schopmeyer and Mergen make the following summarization:

"Each of the three factors in the product, $\frac{N(ab)^2}{H}$ where N = number of radial resin ducts per unit area of wound surface a and b = semi-axis of the resin duct openings H = viscosity of gum, made a significant contribution to the magnitude of flow rate of oleoresin from punch wounds during the first 24 hours after wounding, in a random sample of 12 slash pine trees.

"The product of the three factors accounted for 88 percent of the variation in flow rate between trees, when the regression line is allowed to deviate from the origin.

"No precision was gained by assuming that the power of each factor differed from unity.

"Exudation pressure of oleoresin was expected to contribute to the magnitude of the flow rate, but the measurements obtained in this study were not true values and hence did not contribute significantly to the precision of the estimated flow rate."

This work now offers for the first time a means by which we can account for the tree to tree variations in resin yield, and it seems quite logical to assume that the results of this investigation will apply to our western pine species. If this latter assumption, and also the assumption that quantitative resin flow governs a tree's insect susceptibility, is substantiated, then it may be possible to find some correlation between the variables given above and the relative beetle susceptibility of different classes of trees - i.e., high- and low-risk ponderosa pine. For example, if the viscosity of the oleoresin of each individual tree is genetically fixed and is constant throughout the life span of the tree, then it is possible that the high risk condition which develops in some trees in a relatively short period of time may be the result of changes in the number and size of the resin ducts alone. On the other hand, if the viscosity fluctuates, seasonally or otherwise, then all three factors may contribute to the change from low to high risk.

The Role of Moisture Tension in Resin Production

In contrast to high and low risk there are cases in which the susceptibility of trees changes from season to season - i.e., young pines and their susceptibility to engraver beetles. It seems most logical to theorize that this latter type of susceptibility would be a function of seasonal fluctuations in the environmental factors affecting the resin producing capacity of all trees, as Schwerdtfeger (1948) has pointed out, rather than seasonal tree to tree fluctuations in each tree's resin system. From the discussion of the preceding sections it is obvious that the seasonal, environmental factors which affect resin production are the tensions of the moisture columns within the tree, to a lesser extent the temperatures of the air and soil, water, and perhaps also the resin viscosity.

The role of the tree's moisture supply in relation to oleoresin synthesis and exudation has never been accurately determined. However, Munch states that:

> "..the alternating tension of the transpiration stream and of the water in the tracheids must have an essential influence on the resin flow. This tension seeks in its turn to deprive the parenchyma cells of water or to obstruct their transpiration, and in this, it contrasts with the osmotic pressure of the cell content."

Apparently, moisture tension has a profound influence on resin exudation. This is shown by the following statements which Ivanov quotes from Votchal:

> "the rate of this exudation depends not only on the primary pressure, the degree of viscosity, and the magnitude of rubbing within the resin ducts, but also depends on the rate of water absorption by the excretory cells. . . . The squeezed excretory cells during the excretion of the resin begin to unfold and press out the resin gradually according to how fast

"they are osmotically absorbing water. This absorption of course is only possible in the presence of free capillary water near these cells."

If the dead layer of cells surrounding the epithelial cells is full of air, as it usually is, then the water for the excretory cells has to be taken from the neighboring tracheids which of course is much more difficult. He further states the reasons for this are that:

"1. The excretory cells do not adjoin the tracheids and are separated from them by a layer of dead inflated cells.

"2. The water in the tracheids, especially in the outer layers, is present in a state of surface tension. Under the influence of the absorption by the roots and consequently in order to be able to take that water it would be necessary to overcome some resistance which is greater as the transpiration is greater.

"In this manner, the exudation of the gum from the resin ducts which have recently been opened could be continued uninterrupted according to the ability of the excretory cells to absorb water from the layer of dead cells. Within the resin ducts, there could occur a retardation of excretion of gum due to the retardation of water absorption by the excretory cells which is closely tied up with the water content of the tree. All the factors that favor the tree would also favor the excretion of gum which is found in its resin ducts. Especially is the relative humidity of the air favorable to the excretion of gum because it reduces the transpiring power of the leaves and concurrently lowers the stress of the water threads in the sapwood. On the contrary, conditions which retard the entrance of water into the excretory cells also retard the excretion of gum."

Ivanov also refers to Votchal's work on measuring resin exudation pressure with manometers in which Votchal found that the pressure during drought is lower but that after rain it begins to rise again. He also found that such changes are more markedly observed in manometers of crowns where the pressure in general is less than down below. This is in general agreement with the theory that moisture tension increases in proportion to the height above ground of the position of sampling.

Presuming that the oleoresin theory of bark-beetle susceptibility is applicable to this problem of seasonal susceptibility, one might study with profit the seasonal fluctuations in resin viscosity, moisture tension, and resin exudation pressure in a number of trees growing under different environmental conditions. One might also study the possible interrelationship of these fluctuations with the susceptibility of these trees to bark beetles. For studies such as these, one should employ jointly a technique for measuring moisture tension, which has been perfected recently by the author (Callaham, 1952a) and a technique for studying soil moisture, which Hall (1940) has used in studying the effects of climate on bark-beetle ecology.

SUMMARY

The oleoresin theory of bark-beetle susceptibility has been presented in another report, and it is the purpose of this report to discuss the theoretical principles of oleoresin production in pines, the various factors which determine quantitative production, and their possible application in studying the susceptibility of pines to bark beetles. With this as a basis, the general principles which govern oleoresin production in all pine species are discussed. The anatomical and physiological bases of oleoresin production and methods of predetermining resin flow are discussed separately.

The discussion points out that the longitudinal and transverse resin ducts of all pine species have essentially the same anatomical structure. The discussion of the physiological basis of oleoresin production points out that the following factors affect this production:

(1) Factors affecting rate of resin flow from the severed canal.
(a) Viscosity of the resin, which varies with temperature.
(b) Osmotic pressure of the epithelial cells, which varies with the compression of the cells and the availability of water to the cells.

(2) Factors affecting the rate of resin formation in the resin duct.
(a) Osmotic pressure of the epithelial cells, which varies as does factor (b) above.
(b) Temperature of the water available to the epithelial cells.
(c) Availability of water to the epithelial cells, which varies with moisture tension.
(d) Availability of nutrients to these cells.

The results of some experiments conducted by C. S. Schopmeyer which can be used in predetermining the rate of resin flow are given. These experiments showed that viscosity, number of ducts, and area of duct openings contribute equally to 68 percent of the variation in gum flow between individual trees. It is suggested that an analysis of these variables in trees of known degrees of beetle susceptibility may show a correlation between the potential resin production rate and beetle susceptibility of a given tree. This then might further substantiate the oleoresin theory of susceptibility to bark beetles.

The role of moisture tension in resin production is discussed, and it is suggested that an analysis of the moisture tension and resin exudation pressure variations during the course of several seasons might give some evidence in support of the theory that adverse environmental conditions cause a reduction in resin production with a corresponding increase in the susceptibility of pines to engraver-beetle attacks.

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